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On the origin of South American populations of the common house gecko (Gekkonidae: *Hemidactylus frenatus*)

Omar Torres-Carvajal[1]

1 *Museo de Zoología, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Avenida 12 de Octubre 1076 y Roca, Apartado 17-01-2184, Quito, Ecuador*

Corresponding author: *Omar Torres-Carvajal* (omartorcar@gmail.com)

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Abstract

Hemidactylus frenatus is an Asian gecko species that has invaded many tropical regions to become one of the most widespread lizards worldwide. This species has dispersed across the Pacific Ocean to reach Hawaii and subsequently Mexico and other Central American countries. More recently, it has been reported from northwestern South America. Using *12S* and *cytb* mitochondrial DNA sequences I found that South American and Galápagos haplotypes are identical to those from Hawaii and Papua New Guinea, suggesting a common Melanesian origin for both Hawaii and South America. Literature records suggest that *H. frenatus* arrived in Colombia around the mid-'90s, dispersed south into Ecuador in less than five years, and arrived in the Galápagos about one decade later.

Keywords

Galápagos, Gekkonidae, *Hemidactylus*, invasive species, South America

Introduction

With more than 120 species occurring in warm regions worldwide, *Hemidactylus* accounts for nearly 13% of the total number of recognized species in the family Gekkonidae. It is one of the most species-rich and widely distributed reptile clades (Carranza

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and Arnold 2006). Nonetheless, species of *Hemidactylus* occur naturally only in Asia, Africa, the Mediterranean region, and South America (Carranza and Arnold 2006) and most of them have small distribution ranges confined to southern Asia and Africa. The enormous geographical range covered by *Hemidactylus* is in fact explained by the distribution of just a few species – *H. angulatus*, *H. brookii*, *H. flaviviridis*, *H. frenatus*, *H. garnotii*, *H. mabouia*, *H. parvimaculatus*, *H. persicus*, and *H. turcicus* (Bauer et al. 2010; Carranza and Arnold 2006; Kluge 1969). Most of them are frequently found in association with human settlements, and some have dispersed transoceanically either by human activity or natural rafting (Šmíd et al. 2013). As alien reptiles, species of *Hemidactylus* can achieve large densities leading to potential changes to food webs and ecosystem dynamics of the invaded areas (Kraus 2009).

The natural range of many of these widespread species is sometimes not clear. The common house gecko, *H. frenatus* Duméril & Bibron, 1836, is thought to have originated in tropical Asia and possibly the Indo-Pacific (Bansal and Karanth 2010; Bauer et al. 2010; Case et al. 1994) and has been introduced on many tropical and subtropical regions worldwide including the Eastern Pacific and mainland South America (Fig. 1), where it seems to be expanding its range. It has been recently reported from Venezuela (Rivas Fuenmayor et al. 2005), Colombia (Caicedo-Portilla and Dulcey-Cala 2011), and Ecuador (Jadin et al. 2009) including the Galápagos Islands (Torres-Carvajal and Tapia 2011). Despite this seemingly rapid range expansion, no attempts have been made to investigate the origin and spread of *H. frenatus*

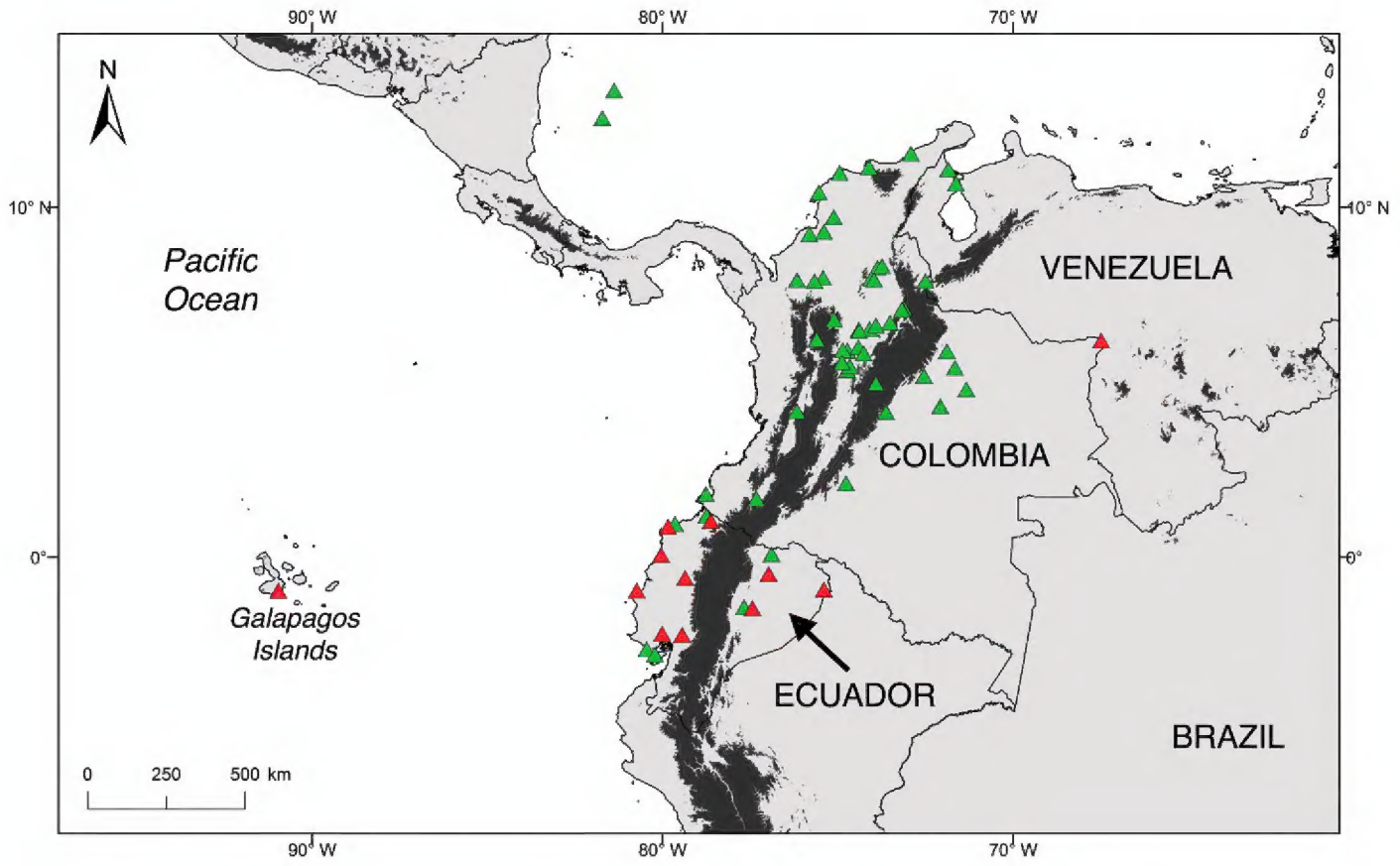

Figure 1. Distribution of *Hemidactylus frenatus* in South America and adjacent islands. Areas above 2000 m are shaded in dark grey. Localities of samples included in this study are shown in red. Locality data was taken from Rivas Fuenmayor et al. (2005), Jadin et al. (2009), Caicedo Portilla and Dulcey-Cala (2011), Torres-Carvajal and Tapia (2011), and the specimen database at Museo de Zoología QCAZ.

throughout the American continent and intervening islands. In this study, I use new mitochondrial DNA sequence data from individuals of *H. frenatus* occurring on mainland Ecuador and the Galápagos along with published sequences from Colombia, Hawaii and Asia to investigate the origin and colonization history of invasive populations of *H. frenatus* in South America. The objectives of my study are (i) to infer a phylogenetic tree of *H. frenatus* from South America, the Eastern Pacific (Galápagos), Hawaii, Melanesia, and Asia, and (ii) use that tree to infer the origin of *H. frenatus* from South America.

Materials and methods

Character and taxon sampling

I obtained nucleotide (nt) sequences of the mitochondrial ribosomal small subunit (*12S*, 370 nt) and cytochrome b (*cytb*, 303 nt) genes from 15 specimens collected on both sides of the Andes in Ecuador, as well as the Galápagos islands, and deposited in the herpetological collection of Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ). In addition, I retrieved sequences from GenBank representing samples of *Hemidactylus frenatus* from Colombia, Hawaii, India, Myanmar and Papua New Guinea. I used *H. brookii* and *H. flaviviridis* as outgroup taxa because they are closely related to *H. frenatus* (Carranza and Arnold 2006). GenBank accession numbers of specimens included in this study are presented in Table 1.

Laboratory protocols

Genomic DNA was isolated from frozen muscle or liver tissues using a guanidinium isothiocyanate extraction protocol. Polymerase Chain Reaction (PCR) amplification of gene fragments was performed in a final volume of 25 µl reactions using 1X PCR Buffer (– Mg), 3 mM $MgCl_2$, 0.2 mM dNTP mix, 0.2 µM of each primer, 0.1 U/µl of Platinum® *Taq* DNA Polymerase (Invitrogen, Carlsbad, CA) and 1 µl of extracted DNA. Negative controls were run on all amplifications to check for contamination. Gene fragments were amplified using the primers 12S1L, 12S2H and 12sb for *12S* (Blair et al. 2009; Kocher et al. 1989) and LGL765, GluDGL and H16064 for *cytb* (Bickham et al. 1995; Burbrink et al. 2000; Palumbi 1996). The amplification protocol consisted of 1 cycle of initial denaturation for 3–5 min at 96 °C, 30–40 cycles of denaturation for 30–40 sec at 92–94 °C, annealing for 30–40 sec at 48–57 °C, and extension for 40–110 sec at 72 °C, as well as a final extension for 7–15 min at 72 °C. Positive PCR products were visualized in agarose electrophoretic gels and treated with ExoSAP-it (Affymetrix, Cleveland, OH) to remove unincorporated primers and dNTPs. Cycle sequencing reactions were carried out by Macrogen Inc. (Seoul, Republic of Korea).

Table 1. Vouchers, locality data, and GenBank accession numbers of taxa and gene regions included in this study. Geographical coordinates in decimal degrees are provided for new localities sampled in this study.

Taxon	Voucher	Locality	GenBank accession number	
			cytb	12S
Hemidactylus brookii	E1109.10	India	DQ120276	DQ120447
H. flaviviridis	E912.2	Yemen	DQ120284	DQ120455
H. frenatus	CES07035	India	HM595655	HM595691
H. frenatus	E509.5	India	DQ120282	DQ120453
H. frenatus	E509.2	Myanmar	DQ120281	DQ120452
H. frenatus	E509.1	Myanmar	DQ120280	DQ120451
H. frenatus	NV	Papua New Guinea	AY217801	AY218005
H. frenatus	E509.7	Hawaii	DQ120278	DQ120449
H. frenatus	E509.6	Hawaii	DQ120277	DQ120448
H. frenatus	E509.3	Colombia	DQ120279	DQ120450
H. frenatus	QCAZ4524	Ecuador: Esmeraldas 1.0425; -78.6304	KT455016	KT455031
H. frenatus	QCAZ4875	Ecuador: Manabí -0.9505; -80.7423	KT455017	KT455032
H. frenatus	QCAZ5076	Ecuador: Esmeraldas 0.8740; -79.8450	KT455018	KT455033
H. frenatus	QCAZ8124	Ecuador: Pastaza -1.4529; -77.4425	KT455019	KT455034
H. frenatus	QCAZ8130	Ecuador: Pastaza -1.4529; -77.4425	KT455020	KT455035
H. frenatus	QCAZ8472	Ecuador: Guayas -2.2126; -79.4472	KT455021	KT455036
H. frenatus	QCAZ9111	Ecuador: Guayas -2.1822; -80.0181	KT455022	KT455037
H. frenatus	QCAZ10197	Ecuador: Pichincha -0.5888; -79.3627	KT455023	KT455038
H. frenatus	QCAZ10213	Ecuador: Orellana -0.4720; -76.9807	KT455024	KT455039
H. frenatus	QCAZ10215	Ecuador: Orellana -0.4720; -76.9807	KT455025	KT455040
H. frenatus	QCAZ11128	Ecuador: Galápagos -0.9573; -90.9674	KT455026	KT455041
H. frenatus	QCAZ11165	Ecuador: Galápagos -0.9573; -90.9674	KT455027	KT455042
H. frenatus	QCAZ11197	Ecuador: Galápagos -0.9573; -90.9674	KT455028	KT455043
H. frenatus	QCAZ11452	Ecuador: Manabí 0.0740; -80.0480	KT455029	KT455044
H. frenatus	QCAZ11593	Ecuador: Orellana -0.9167; -75.4000	KT455030	KT455045

Alignment, model selection, and phylogenetic analyses

Data were aligned in MAFFT under default settings (Katoh and Toh 2010). Genes were combined into a single matrix with four partitions (*12S* and 1st, 2nd and 3rd codon positions of *cytb*). Evolutionary models for each partition were selected using jMODELTEST (Posada 2008) under the Bayesian information criterion. Phylogenetic relationships were assessed under a Bayesian approach in MrBAYES 3.2.0 (Ronquist and Huelsenbeck 2003). The analysis consisted of ten million generations and four Markov chains with default heating values. Trees were sampled every 1000 generations resulting in 10000 saved trees per analysis. Convergence was confirmed by plotting the –ln *L* per generation. Adequacy of mixing was assessed by examining the acceptance rates for the parameters in MrBAYES; I verified that the average standard deviation of split frequencies between chains and the potential scale reduction factor (PSRF) of all the estimated parameters approached values of ≤ 0.01 and 1, respectively. Additionally, I used TRACER to verify that the effective sample sizes (ESS) had values above 200. After analyzing convergence and mixing, 1000 trees were discarded as "burn-in" from each run. We used the resultant 36,000 trees to calculate posterior probabilities (PP) for each bipartition on a 50% majority rule consensus tree. Intra- and interspecific sequence divergence for each gene was assessed with uncorrected distances, which were obtained in PAUP* (Swofford 2003).

Results

A total of 673 aligned sites of *12S* (370 nt) and *cytb* (303 nt) were obtained. Selected models were K80+G, 000010+F, TrN, and 012212+G+F for 1st, 2nd and 3rd codon positions of *cytb* and *12S*, respectively. Of the 25 aligned sequences, 17 contained missing data ranging between 1–65 sites, which together represented 2.6% of the total sites in the matrix.

All 15 new sequences obtained in this study from continental Ecuador and the Galápagos, as well as GenBank sequences of specimens from Colombia, Hawaii and Papua New Guinea were identical (missing data ignored). The clade formed by these sequences (PP=0.95) was recovered with high support (PP=0.91) as sister to a clade with two samples from Myanmar (PP=0.90); samples from India were nested in a clade (PP=0.78) sister to all other samples of *Hemidactylus frenatus* (Fig. 2). Monophyly of this species was not supported strongly (PP=0.65). The same phylogenetic analysis as described above, except that identical sequences were removed, yielded slightly higher posterior probability values.

Intraspecific genetic distances between individuals of *H. frenatus* from Papua New Guinea/Hawaii/South America and individuals from India and Myanmar included in the analysis varied between 0.069–0.132 and 0.047–0.078 for *cytb* and *12S*, respectively (Table 2).

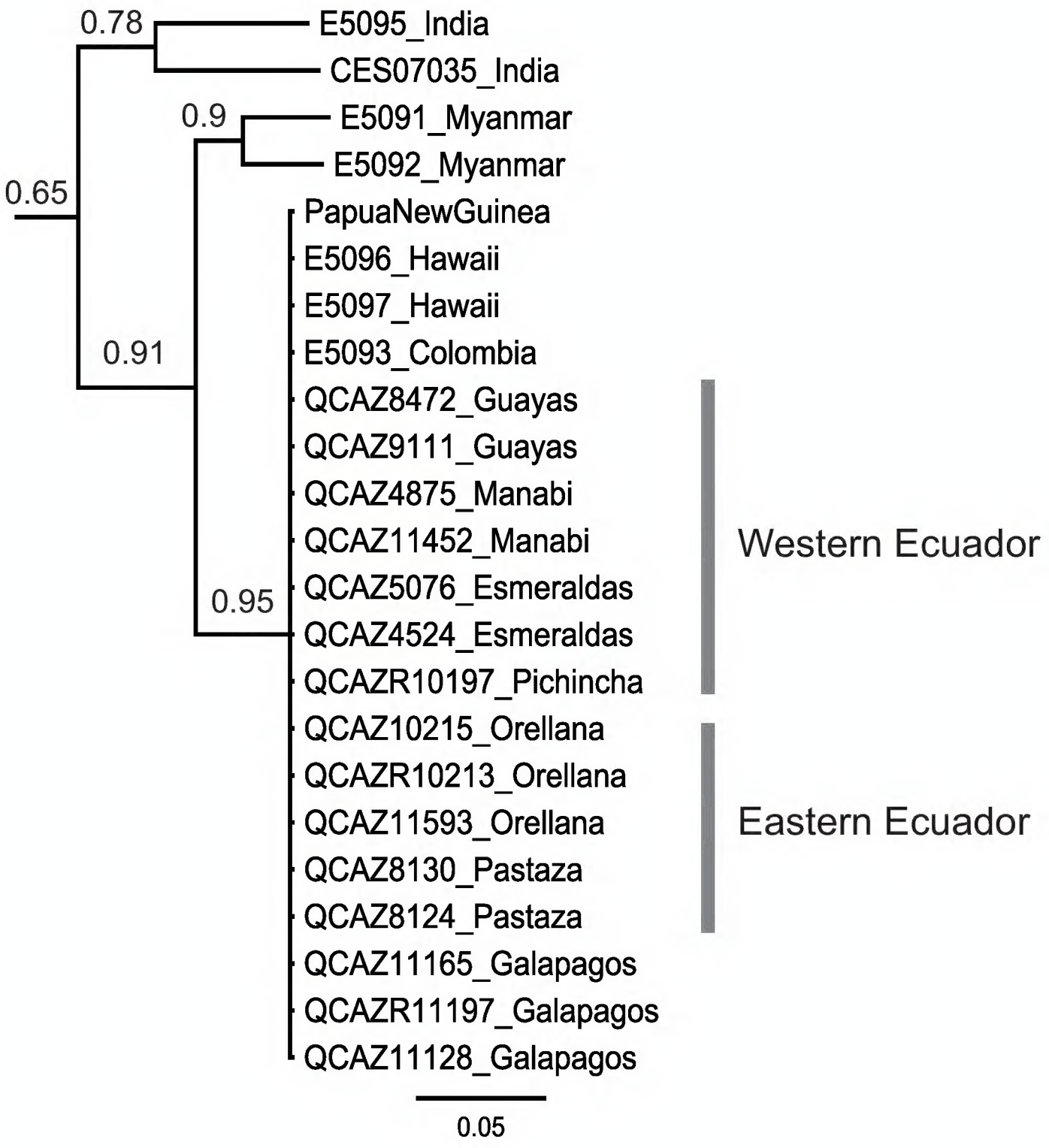

Figure 2. Majority rule (50%) consensus tree of 36,000 trees obtained from a Bayesian analysis of 25 specimens and 673 nucleotides corresponding to *cytb* and *12S* mitochondrial gene regions. Outgroup taxa *Hemidactylus brookii* and *H. flaviviridis* are not shown; all terminals correspond to *H. frenatus*. Numbers on branches are posterior probability values. Voucher numbers (if available) and country of collection are shown on each terminal. For samples collected in Ecuador, voucher numbers and province names are indicated.

Table 2. Uncorrected genetic distances among taxa included in this study for *cytb* (upper diagonal) and *12S* (lower diagonal) gene fragments. Taxon name along with voucher number and country of collection are indicated in first column. The sequence of *H. frenatus* from Colombia represents other sequences from South America, as well as those from Hawaii and Papua New Guinea included in this study.

Taxon sample	1	2	3	4	5	6	7
1: *H. flaviviridis* E912.2 Yemen		0.251	0.201	0.205	0.191	0.218	0.187
2: *H. brookii* E1109.10 India	0.208		0.178	0.195	0.162	0.185	0.189
3: *H. frenatus* E509.1 Myanmar	0.172	0.158		0.076	0.076	0.129	0.130
4: *H. frenatus* E509.2 Myanmar	0.174	0.160	0.025		0.069	0.135	0.105
5: *H. frenatus* E509.3 Colombia	0.175	0.158	0.047	0.047		0.132	0.105
6: *H. frenatus* E509.5 India	0.168	0.151	0.056	0.064	0.078		0.105
7: *H. frenatus* CES07035 India	0.177	0.164	0.078	0.081	0.070	0.061	

Discussion

The fact that *cytb* and *12S* haplotypes of *Hemidactylus frenatus* from Hawaii, the Galápagos, and mainland South America are identical to those in Papua New Guinea sheds some light on the origin and dispersal of this species from Melanesia to South America across the Pacific Ocean. The invasive populations in Hawaii and South America most likely originated from a single 'stock' in Melanesia; otherwise, we would expect more genetic variation among invasive samples. This is supported by the genetic variation that was observed only among the four samples from India and Myanmar included in this study. Although these four samples come from geographically close localities, their genetic distances vary between 0.076–0.135 and 0.025–0.064 for *cytb* and *12S*, respectively (Table 2). Had South American and Hawaiian haplotypes originated from two or more different Melanesian 'stocks', we would observe some degree of genetic divergence when comparing those haplotypes. This contrasts with the high genetic diversity of invasive *H. frenatus* recently reported from the remote Pacific island of Moorea, French Polynesia (Tonione et al. 2011), and shows that invasive species can have different colonization patterns (i.e., one versus multiple invasive haplotypes) across their non-native distribution ranges.

How *Hemidactylus frenatus* arrived in South America remains an open question given its ability for massive, human-mediated range expansion (Carranza and Arnold 2006). One possibility is that this species departed from the same site in Melanesia more than once, arriving both in Hawaii and South America independently. Although I did not investigate marine trading routes in detail, there is probably a better chance that *H. frenatus* first arrived in Hawaii and from there spread (directly or through Central America) to South America.

The common house gecko, as its name suggests, is easy to spot at human settlements feeding around light bulbs at night. Therefore, we can assume that the first time it is found as an invasive species in a certain location corresponds approximately to the colonization time at that location. Thus, based on the year *H. frenatus* was first reported from each site included in this study, it seems like its general colonization route after leaving Papua New Guinea or somewhere nearby was (first report year follows each site) Hawaii 1940s (Kraus 2009), continental Colombia 1996 (Caicedo-Portilla and Dulcey-Cala 2011), continental Ecuador 2000 (QCAZ 6098, 6111) and the Galápagos 2011 (Torres-Carvajal and Tapia 2011). However, colonization in Colombia was probably earlier than 1996 through harbors in the Atlantic Ocean (Caicedo-Portilla and Dulcey-Cala 2011). Regardless of colonization routes, literature data indicate that *H. frenatus* has colonized South America fairly recently, arriving in Colombia first and then spreading south into Ecuador and the Galápagos (Fig. 1). Furthermore, *H. frenatus* was first reported from Venezuela near the Colombian border in 2000 (Rivas Fuenmayor et al. 2005), suggesting that this population also arrived from Colombia.

Recent arrival of *Hemidactylus frenatus* to South America including iconic conservation sites as the Galápagos archipelago should be of concern. Given its great dispersal ability and potential distribution (Rödder et al. 2008), *H. frenatus* is expected to rapidly expand its range across South America. This is an aggressive species that tends to reach high densities and outcompete other lizard species. For example, exclusion of the alien species *Lepidodactylus lugubris* by more recently introduced *H. frenatus* has been documented in several Pacific islands (Bolger and Case 1992; Brown et al. 2002; Cole et al. 2005; Petren et al. 1993; Petren and Case 1998). This competitive exclusion seems to be the result of many factors including behavioral interference, predation on juveniles of *L. lugubris*, enhanced ability of *H. frenatus* to exploit food resources, and avoidance of *H. frenatus* by *L. lugubris* (Kraus 2009). Endemic lizard species can also be negatively affected by invasive common house geckos, as has been shown in the Mascarene islands, where the arrival of *H. frenatus* resulted in population declines and even some extinction events of the native *Nactus* geckos (Cole et al. 2005). Besides competition, invasive *H. frenatus* can have negative secondary trophic effects. For example, *H. frenatus* is one of the alien prey species that help the invasive snake *Boiga irregularis* maintain high densities in Guam (Fritts and Rodda 1998).

Only recently was *Hemidactylus frenatus* reported for the first time in Galápagos (Torres-Carvajal and Tapia 2011). It was collected on Isabela Island, where three other

nocturnal lizards are known to occur. One of them is an endemic species of leaf-toed gecko (*Phyllodactylus* sp.; Torres-Carvajal et al. 2014), and the other two are alien nocturnal geckos, the mourning gecko, *Lepidodactylus lugubris*, and the South American leaf-toed gecko, *P. reissii* (Hoogmoed 1989; Phillips et al. 2012). As much as this offers a great opportunity to study ecological interactions among one endemic and three invasive species of gecko lizards, it also raises concerns about the conservation status of the endemic species in Isabela and other islands in the archipelago. In lieu of the potential negative impacts of introduced common house geckos presented above, their eradication from the Galápagos archipelago should be seriously considered.

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References

Bansal R, Karanth KP (2010) Molecular phylogeny of *Hemidactylus* geckos (Squamata: Gekkonidae) of the Indian subcontinent reveals a unique Indian radiation and an Indian origin of Asian house geckos. Molecular Phylogenetics and Evolution 57: 459–465. doi: 10.1016/j.ympev.2010.06.008

Bauer AM, Jackman TR, Greenbaum E, Giri VB, de Silva A (2010) South Asia supports a major endemic radiation of *Hemidactylus* geckos. Molecular Phylogenetics and Evolution 57: 343–352. doi: 10.1016/j.ympev.2010.06.014

Bickham JW, Wood CC, Patton JC (1995) Biogeographic implications of cytochrome b sequences and allozymes in sockeye (*Oncorhynchus nerka*). Journal of Heredity 86: 140–144.

Blair C, Mendez de la Cruz FR, Ngo A, Lindell J, Lathrop A, Murphy RW (2009) Molecular phylogenetics and taxonomy of leaf-toed geckos (Phyllodactylidae: *Phyllodactylus*) inhabiting the peninsula of Baja California. Zootaxa 2027: 28–42.

Bolger DT, Case TJ (1992) Intra- and interspecific interference behaviour among sexual and asexual geckos. Animal Behaviour 44: 21–30. doi: 10.1016/S0003-3472(05)80750-X

Brown SG, Lebrun R, Yamasaki J, Ishii-Thoene D (2002) Indirect competition between a resident unisexual and an invading bisexual gecko. Behaviour 139: 1161–1173. doi: 10.1163/15685390260437317

Burbrink FT, Lawson R, Slowinski JB (2000) Mitochondrial DNA phylogeography of the polytypic North American rat snake (*Elaphe obsoleta*): a critique of the subspecies concept. Evolution 54: 2107–2118. doi: 10.1111/j.0014-3820.2000.tb01253.x

Caicedo-Portilla R, Dulcey-Cala CJ (2011) Distribución del gecko introducido *Hemidactylus frenatus* (Duméril y Bibron 1836) (Squamata: Gekkonidae) en Colombia. Biota Colombiana 12: 45–56.

Carranza S, Arnold EN (2006) Systematics, biogeography, and evolution of *Hemidactylus* geckos (Reptilia: Gekkonidae) elucidated using mitochondrial DNA sequences. Molecular Phylogenetics and Evolution 38: 531–545. doi: 10.1016/j.ympev.2005.07.012

Case TJ, Bolger DT, Petren K (1994) Invasions and competitive displacement among House Geckos in the Tropical Pacific. Ecology 75: 464–477. doi: 10.2307/1939550

Cole NC, Jones CG, Harris S (2005) The need for enemy-free space: the impact of an invasive gecko on island endemics. Biological Conservation 125: 467–474. doi: 10.1016/j.biocon.2005.04.017

Fritts TH, Rodda GH (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. Annual Review of Ecology and Systematics 29: 113–140. doi: 10.1146/annurev.ecolsys.29.1.113

Hoogmoed MS (1989) Introduced geckos in Puerto Ayora, Santa Cruz, with remarks on other areas. Noticias de Galapagos 47: 12–16.

Jadin RC, Altamirano M, Yánez-Muñoz M, Smith EN (2009) First record of the common house gecko (*Hemidactylus frenatus*) in Ecuador. Appl Herpetology 6: 193–195. doi: 10.1163/157075408X394133

Katoh K, Toh H (2010) Parallelization of the MAFFT multiple sequence alignment program. Bioinformatics 26: 1899–1900. doi: 10.1093/bioinformatics/btq224

Kluge AG (1969) The evolution and geographical origin of the New World *Hemidactylus mabouia-brookii* complex (Gekkonidae, Sauria). Miscellaneous publications, Museum of Zoology, University of Michigan 138: 1–78.

Kocher TD, Thomas WK, Meyer A, Edwards SV, Pääbo S, Villablanca FX, Wilson AC (1989) Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proceedings of the National Academy of Sciences of the United States of America 86: 6196–6200. doi: 10.1073/pnas.86.16.6196

Kraus F (2009) Alien reptiles and amphibians: A scientific compendium and analysis. Springer, New York, 563 pp. doi: 10.1007/978-1-4020-8946-6

Palumbi SR (1996) Nucleic acids II: the polymerase chain reaction. In: Hillis DM, Moritz C, Mable BK (Eds) Molecular Systematics. Sinauer, Sunderland, Massachusetts, 205–247.

Petren K, Bolger DT, Case TJ (1993) Mechanisms in the competitive success of an invading sexual gecko over an asexual native. Science 259: 354–358. doi: 10.1126/science.259.5093.354

Petren K, Case TJ (1998) Habitat structure determines competition intensity and invasion success in gecko lizards. Proceedings of the National Academy of Sciences of the United States of America 95: 11739–11744. doi: 10.1073/pnas.95.20.11739

Phillips RB, Wiedenfeld D, Snell H (2012) Current status of alien vertebrates in the Galapagos Islands: invasion history, distribution, and potential impacts. Biological Invasions 14: 461–480. doi: 10.1007/s10530-011-0090-z

Posada D (2008) jModelTest: Phylogenetic Model Averaging. Molecular Biology and Evolution 25: 1253–1256. doi: 10.1093/molbev/msn083

Rivas Fuenmayor G, Ugueto GN, Bauer AM, Barros T, Manzanilla J (2005) Expansion and natural history of a successful colonizing gecko in Venezuela (Reptilia: Gekkonidae: *Hemidactylus mabouia*) and the discovery of *H. frenatus* in Venezuela. Herpetological Review 36: 121–125.

Rödder D, Solé M, Böhme W (2008) Predicting the potential distributions of two alien invasive Housegeckos (Gekkonidae: *Hemidactylus frenatus*, *Hemidactylus mabouia*). North-Western Journal of Zoology 4: 236–246.

Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. Bioinformatics 19: 1572–1574. doi: 10.1093/bioinformatics/btg180

Šmíd J, Carranza S, Kratochvil L, Gvoždík V, Nasher AK, Moravec J (2013) Out of Arabia: a complex biogeographic history of multiple vicariance and dispersal events in the gecko genus *Hemidactylus* (Reptilia: Gekkonidae). PLoS ONE 8: e64018. doi: 10.1371/journal.pone.0064018

Swofford DL (2003) PAUP* Phylogenetic Analysis Using Parsimony (*and Other Methods), v. 4. Sinauer Associates, Sunderland.

Tonione MA, Reeder N, Moritz CC (2011) High genetic diversity despite the potential for stepping-stone colonizations in an invasive species of gecko on Moorea, French Polynesia. PLoS ONE 6: e26874. doi: 10.1371/journal.pone.0026874

Torres-Carvajal O, Barnes CW, Pozo-Andrade MJ, Tapia W, Nicholls G (2014) Older than the islands: origin and diversification of Galápagos leaf-toed geckos (Phyllodactylidae: *Phyllodactylus*) by multiple colonizations. Journal of Biogeography 41: 1883–1894. doi: 10.1111/jbi.12375

Torres-Carvajal O, Tapia W (2011) First record of the common house gecko *Hemidactylus frenatus* Schlegel, 1836 and distribution extension of *Phyllodactylus reissii* Peters, 1862 in the Galápagos. Check List 7: 470–472